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APHID TRANSMISSION OF CAULIFLOWER-MOSAIC VIRUS¹

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SUMMARY

ELEVEN SPECIES OF APHIDS that do not multiply on cauliflower plants in nature were demonstrated to be vectors of the cauliflower-mosaic virus, five of them being more efficient vectors than three aphid species that do breed on cauliflower.

Of three aphid species that breed on cauliflower under natural conditions, the cabbage aphid, *Brevicoryne brassicae* (Linnaeus), was a more efficient vector of the virus (in single-insect tests) than the turnip or false cabbage aphid, *Rhopalosiphum pseudobrassicae* (Davis), and the green peach aphid, *Myzus persicae* (Sulzer).

Natural infectivity of the cabbage aphid was demonstrated.

None of twenty-one varieties of cauliflower experimentally infected with the virus by the cabbage and green peach aphids was resistant to the disease.

Mechanical inoculation was more efficient than transmission by the cabbage, turnip, or green peach aphid.

In tests with hourly transfers, most transmissions occurred within 2 hours after the aphids had fed on a mosaic-infected plant.

Aphids acquired the virus in 15 to 25 minutes on a diseased plant (5 to 10 minutes actual feeding time) and transmitted it in feeding periods as short as 5 or 10 minutes. In tests with short feeding periods, most of the transmissions occurred during the first 10 minutes after transfer from the infected plant, but an occasional aphid transmitted the disease during the second or third 10-minute period.

The cabbage and green peach aphids recovered the virus from inoculated cauliflower plants many days before the first symptom appeared.

Mechanical inoculation of healthy cauliflower seedlings and annual stock plants with the centrifuged virus extract from crushed, infective cabbage aphids produced 18 per cent infection.

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INTRODUCTION

Cauliflower is naturally infected with cauliflower mosaic in California (Tompkins, 1934a)⁴ and in Oregon (Tompkins, 1937). Cauliflower plants have been experimentally infected with cauliflower-mosaic virus by mechanical inoculation (Tompkins, 1934a). The host range and properties of the virus have been reported (Tompkins, 1937).

Cauliflower-mosaic virus is transmitted by the cabbage aphid, *Brevicoryne brassicae* Linnaeus, and the green peach aphid, *Myzus persicae* (Sulzer) (Tompkins, 1934a, 1937). Keicola (1945) demonstrated that *M. persicae* and *B. brassicae*, when colonized on cauliflower seedlings infected with both cabbage black ringspot (cabbage ringspot) and cauliflower mosaic, transmitted both viruses; whereas *M. ornatus*, when similarly colonized, transmitted only the cauliflower-mosaic virus.

An investigation was undertaken to obtain further information on aphid transmission of the cauliflower-mosaic virus. Tests were made both with species that do not breed on cauliflower under natural conditions and with species that do. Other aspects investigated include the efficiency in the transmission of the virus by single aphids and by varying numbers of aphids; susceptibility of cauliflower varieties to the disease; comparative efficiency of mechanical inoculation and aphid transmission; the natural infectivity of the aphids; retention of the virus by aphids; and whether infections could be obtained with the virus extract from crushed, infective aphids.

In a companion paper, Essig (1948) discusses the characters, distribution, and food plants of aphid species which occur on cauliflower plants under natural conditions in California.

Leafhoppers transmit two other viruses to cauliflower: cauliflower plants experimentally infected with the curly-top virus by means of the beet leafhopper, *Eutettix tenellus* (Baker), developed symptoms, though noninfective leafhoppers failed to recover the virus (Severin, 1929); and California aster yellows has been recovered from naturally infected cauliflower and transferred to healthy aster and celery plants by previously noninfective aster leafhoppers, *Macrosteles divisus* (Uhler) (Severin and Frazier, 1945). Hence, tests of cauliflower-mosaic virus transmission by species of leafhoppers were included in this investigation. Transmission by a plant bug naturally occurring on cauliflower was also tested.

MATERIALS AND METHODS

The virus was obtained from severely stunted plants of the February variety of cauliflower at Alvarado. It was maintained by repeated mechanical inoculation and aphid transmission of the virus to healthy February cauliflower and Fiery Blood Red annual stock plants. The carborundum method (Rawlins and Tompkins, 1936) was used in mechanical inoculations.

Colonies of noninfective aphid species were started by transferring mature, wingless aphids from cauliflower, cabbage, or stock to Esmarch dishes with the bottoms covered with moist filter paper. The young aphids were then placed on healthy cauliflower or annual stock plants grown from seeds. The

⁴ See "Literature Cited" for citations, referred to in the text by author and date.

method of transferring aphids has been published in a previous paper (Severin and Freitag, 1938). The preparation of the virus extract from crushed, infective aphids and by centrifugation was similar to the method described for the beet leafhopper (Severin and Freitag, 1933).



Fig. 1. Local symptoms of cauliflower mosaic on leaves of cauliflower seedling, on which the cabbage aphid had fed, showing chlorotic areas around mouth-part punctures.

SYMPTOMATOLOGY

A general description of the symptoms of cauliflower mosaic on several host plants including annual stock was given in a previous paper (Tompkins, 1937) : clearing of the veins was the predominant symptom; stunting was not observed. The average incubation period of the disease on Fiery Blood Red annual stock (*Mathiola incana* var. *annua*) was 70 days.

In cauliflower, mosaic is characterized by stunting of the plant, dwarfing of the terminal head or curd, and the following leaf symptoms : vein clearing (plate 1, *B*) ; curvature of the midrib (plate 1, *D*) ; necrotic lesions (plate 1, *E*, *F*) and distortion of the leaf (plate 1, *G*).

Feeding by the cabbage aphid causes symptoms on cauliflower, aside from those caused by the virus. The leaves of cauliflower seedlings on which either noninfective or infective cabbage aphids had fed showed circular chlorotic areas around the mouth-part punctures (fig. 1). The newly developing leaves on which no aphids had fed failed to show this symptom ; hence the effect is local and not systemic. Other species of aphids do not cause this symptom.

Since annual stock has been experimentally infected with five crucifer viruses (Tompkins, 1934b, 1937, 1938, 1939; Tompkins, Gardner, and Thomas, 1938), a detailed description of the successive foliage symptoms of cauliflower mosaic on stock is given to distinguish this virus disease from others, especially from mild and severe mosaics of stock plants, described in a previous paper (Tompkins, 1939). The first symptom that appears on the youngest leaves of Fiery Blood Red annual stock is a clearing of the veins and veinlets (plate 2, C), followed by the development of numerous chlorotic, circular areas (plate 2, D), producing a mottled effect (plate 2, E). The veins may protrude on the lower surface of the leaf (plate 1, F). A shortening of the internodes occurs, and secondary shoots develop with dwarfed leaves cupped inward along the midrib (plate 2, A).

TESTS WITH PLANT BUGS AND LEAFHOPPERS

Tests were made to determine whether plant bugs and leafhoppers occurring in cauliflower fields could transmit the virus of cauliflower mosaic. The harlequin cabbage bug, *Murgantia histrionica* (Hahn), was abundant on cauliflower plants in San Pablo. Lots of 2 to 5 adults were transferred, alternating daily from mosaic to healthy cauliflower plants. No infections occurred with 30 cauliflower plants tested. No infections were obtained with the beet leafhopper, short-winged and long-winged aster leafhoppers, *Macrostelus divisus* (Uhler); the geminate leafhopper, *Colladonus geminatus* (Van Duzee); or the mountain leafhopper, *C. montanus* (Van Duzee).

APHID TRANSMISSION OF VIRUS

By Vectors That Do Not Breed on Cauliflower. Aphids that have not been found to breed on cauliflower plants under natural conditions were tested for transmission of the virus of cauliflower mosaic. The aphids were transferred singly, directly from diseased plants to healthy cauliflower seedlings, one aphid to a plant, and were kept on the healthy plants until they died. Most of the species tested proved capable of transmitting the virus (table 1). There was a considerable variation in the percentages of virus transmission by the different species. The most important vectors were the pea aphid, *Macrosiphum pisi* (Kaltenbach); celery aphid, *Aphis apii* Theobald; lily aphid, *Myzus circumflexus* (Buckton); and yellow willow aphid, *Cavariella capreae* (Fabricius). Others that transmitted the virus were the celery leaf aphid, *Aphis apigraveolens* Essig; rusty-banded aphid, *Aphis ferruginea-striata* Essig; cotton or melon aphid, *Aphis gossypii* Glover; erigeron root aphid, *Aphis middletonii* (Thomas); foxglove aphid, *Myzus solani* (Kaltenbach); and honeysuckle aphid, *Rhopalosiphum conii* (Davidson). The bean or dock aphid, *Aphis rumicis* Linnaeus, failed to transmit the virus. It may be possible that species of winged aphids play an important role in the dissemination of the virus.

By Single Aphids Breeding on Cauliflower. Three aphid species that breed on cauliflower under natural conditions were tested for efficiency as vectors of the virus; these were the cabbage aphid, *Brevicoryne brassicae* (Linnaeus);

⁵ According to E. O. Essig (personal interview), *Aphis apii* Theobald may be identical with *A. helianthi* Monell.

turnip or false cabbage aphid, *Rhopalosiphum pseudobrassicae* (Davis); and green peach aphid, *Myzus persicae* (Sulzer). Tests were made with wingless and winged aphids, reared to maturity on mosaic-infected cauliflower and then transferred, each to a separate healthy cauliflower plant. Table 2 compares the number of infections obtained with single winged and wingless aphids. Of the three species of aphids tested singly, the cabbage aphid is the most efficient vector of the virus.

TABLE 1
TRANSMISSION OF CAULIFLOWER-MOSAIC VIRUS BY
SINGLE APHID SPECIES

Species of aphids	Cauliflower		Per cent infected
	Inoculated	Infected	
Celery leaf aphid, <i>Aphis apigraveolens</i>	35	2	6
Celery aphid, <i>Aphis apii</i> *.....	35	25	71
Rusty-banded aphid, <i>Aphis ferruginea-striata</i>	85	4	5
Cotton or melon aphid, <i>Aphis gossypii</i>	50	2	4
Erigeron root aphid, <i>Aphis middletonii</i>	75	1	1
Bean or dock aphid, <i>Aphis rumicis</i>	80	0	0
Yellow willow aphid, <i>Cavariella capreae</i>	35	20	57
Pea aphid, <i>Macrosiphum pisi</i>	35	30	86
Lily aphid, <i>Myzus circumflexus</i>	35	23	66
Foxglove aphid, <i>Myzus convolvuli</i>	35	10	29
Honeysuckle aphid, <i>Rhopalosiphum conii</i>	50	1	2

See footnote 5, page 392.

TABLE 2
TRANSMISSION OF VIRUS BY SINGLE APHIDS THAT BREED ON
CAULIFLOWER UNDER NATURAL CONDITIONS

Species of aphids	Results with wingless mature aphids			Results with winged aphids		
	Cauliflower			Cauliflower		
	Inoculated	Infected	Per cent infected	Inoculated	Infected	Per cent infected
Cabbage aphid, <i>Brevicoryne brassicae</i>	150	28	15	100	22	22
Turnip aphid, <i>Rhopalosiphum pseudobrassicae</i>	200	8	4	100	5	5
Green peach aphid, <i>Myzus persicae</i>	100	11	11	150	4	3

From Naturally Infected Cauliflower and Brussels Sprouts. Whenever high populations of the cabbage aphid were found on mosaic-infected cauliflower plants, lots of 20 aphids were transferred to healthy cauliflower and annual stock plants. Table 3 shows the counties and districts from which the source of virus was obtained. The cabbage aphid transmitted the virus to 67 per cent of the cauliflower and to 43 per cent of the annual stock plants. Virus from the Richmond and Colma districts was transmitted to cauliflower but not to stock.

The virus was also transmitted by the cabbage aphid from naturally infected brussels sprouts obtained at El Granda to healthy cauliflower seedlings.

From Experimentally Infected Cauliflower to Healthy Cauliflower and Stock Plants. Lots of 20 cabbage, turnip, and green peach aphids were used in determining the transmission of the virus from mosaic-infected cauliflower to healthy cauliflower seedlings and annual stock plants. Table 4 shows the number and percentages of cauliflower and annual stock plants infected with the virus by means of three species of aphids.

TABLE 3
TRANSMISSION OF CAULIFLOWER-MOSAIC VIRUS FROM NATURALLY INFECTED TO HEALTHY CAULIFLOWER AND STOCKS BY LOTS OF 20 CABBAGE APHIDS, *BREVICORYNE BRASSICAE*

County and district	Cauliflower		Stocks	
	Inoculated	Infected	Inoculated	Infected
Alameda county:				
Alameda.....	6	3	6	2
Contra Costa County:				
Richmond.....	6	2	6	0
San Pablo.....	6	6	6	4
San Francisco County:				
San Francisco.....	6	3	6	4
San Mateo County:				
Colma.....	6	6	6	4
El Granada.....	6	4	6	0
Monterey County:				
Salinas.....	6	4	6	4
Total.....	42	28	42	18
Percentage.....	67	43

Annual stock plants infected with the virus by the three species of aphids did not show breaking in the color of the petals, as previously reported (Tompkins, 1937). Breaking in the flowers of annual stock is caused by two other viruses (Tompkins, 1934b, 1939a).

SUSCEPTIBILITY OF VARIETIES OF CAULIFLOWER

Plants of twenty-one varieties of cauliflower were inoculated with the virus to ascertain whether any variety was resistant to the disease. Lots of 20 infective cabbage aphids and green peach aphids were transferred from diseased to healthy cauliflowers, one lot to a plant. Table 5 shows that 78 per cent of the cauliflower seedlings were infected by means of the cabbage aphid and 58 per cent by the green peach aphid. Again, the cabbage aphid was a more efficient vector of the virus than the green peach aphid. All varieties of cauliflower were highly susceptible to cauliflower mosaic.

COMPARATIVE EFFICIENCY OF MECHANICAL INOCULATION AND APHID TRANSMISSION OF VIRUS

The transmission of virus from experimentally infected to healthy cauliflower plants by mechanical inoculation was compared with transmissions by three species of aphids. A summary of virus transmission by aphids (single

TABLE 4

TRANSMISSION OF CAULIFLOWER-MOSAIC VIRUS FROM INFECTED
CAULIFLOWER TO HEALTHY CAULIFLOWER SEEDLINGS AND
ANNUAL STOCKS BY THREE APHID SPECIES

Aphid species and test no.	Cauliflower		Stocks	
	Inoculated	Infected	Inoculated	Infected
<i>Cabbage aphid, Brevicoryne brassicae:</i>				
Test 1.....	10	0	10	9
Test 2.....	5	5	5	5
Test 3.....	5	5	5	3
Test 4.....	5	5	5	3
Test 5.....	5	4	5	5
Test 6.....	5	3	5	2
Test 7.....	5	3	5	0
Total.....	40	25	40	27
Percentage.....	63	69
<i>Turnip aphid, Rhopalosiphum pseudobrassicae:</i>				
Test 1.....	5	3	5	3
Test 2.....	5	3	5	3
Test 3.....	5	3	5	3
Test 4.....	5	3	5	1
Test 5.....	5	2	5	3
Test 6.....	5	0	5	3
Total.....	30	14	30	16
Percentage.....	47	63
<i>Green peach aphid, Myzus persicae:</i>				
Test 1.....	10	10	10	9
Test 2.....	5	5	5	5
Test 3.....	5	5	5	2
Test 4.....	5	4	5	5
Test 5.....	5	4	5	3
Test 6.....	5	3	5	3
Test 7.....	5	2	5	1
Test 8.....	5	3	5	0
Total.....	45	36	45	28
Percentage.....	80	62

and multiple lots) was taken from tables 3, 4, 5 (February cauliflower), and 7. The virus was maintained by repeated mechanical inoculation and aphid transmission. The virus from the same infected plants upon which the aphids had fed was mechanically inoculated into healthy plants. A comparison of the results obtained is given in table 6. It is evident that the three species of aphids were less efficient than mechanical inoculation in transmitting the virus: 89 to 90 per cent of the healthy cauliflower plants became infected when mechanically inoculated; 43 to 67 per cent when the virus was transmitted by aphids.

TABLE 5

TRANSMISSION OF CAULIFLOWER-MOSAIC VIRUS TO VARIETIES OF
 CAULIFLOWER BY CABBAGE APHID (*BREVICORYNE BRASSICAE*)
 AND GREEN PEACH APHID (*MYZUS PERSICAE*)

Variety of cauliflower	Cabbage aphid		Green peach aphid	
	Plants inoculated	Plants infected	Plants inoculated	Plants infected
April.....	10	9	10	8
February.....	10	10	10	6
Danish Perfection.....	10	10	10	5
December.....	10	7	10	9
Dryweather Danish.....	10	8	20	9
Early March.....	10	6	10	1
Early Snowball.....	10	3	10	7
Extra Early Dwarf Erfurt.....	10	6	10	5
Hartmans Special Early.....	10	10	10	9
Hartmans Special Median.....	10	9	20	8
January.....	10	10	10	7
Late March.....	10	3	10	2
Late Pearl.....	10	6	10	9
November.....	10	10	10	8
St. Valentine.....	10	7	10	9
Super Snowball.....	10	9	10	4
February 759*.....	10	10	10	5
Christmas 2022*.....	20	16	20	8
Early March 713*.....	10	8	10	3
Early March 767*.....	10	9	10	7
Mission Special*.....	10	5	10	9
Total.....	220	171	240	138
Percentage.....	78	58

* The cauliflowers were grown from seeds from Ferry-Morse Seed Co., San Francisco.

TABLE 6

COMPARISON OF TRANSMISSION OF CAULIFLOWER-MOSAIC VIRUS BY
 MECHANICAL INOCULATION WITH THREE SPECIES OF APHIDS

Number of plants from which virus was recovered	Mechanical inoculation			Aphids	Aphid transmission		
	Plants inoculated	Plants infected	Per cent infected		Plants inoculated	Plants infected	Per cent infected
27	125	112	90	Cabbage aphid, <i>Brevicoryne brassicae</i>	165	110	67
12	70	63	90	Turnip aphid, <i>Rhopalosiphum pseudobrassicae</i>	70	30	43
20	120	107	89	Green peach aphid, <i>Myzus persicae</i>	120	69	58

RETENTION OF VIRUS

By Varying Numbers of Aphids with Daily Transfers. The retention of the virus was determined with three species of aphids reared on mosaic-infected cauliflower plants. In most tests, lots of 20 aphids were used; but occasionally 10, 5, and single aphids were employed. Each lot of aphids was transferred daily, usually for three days, to successive healthy cauliflower seedlings. In preliminary work the aphids sometimes were transferred daily

TABLE 7
RETENTION OF CAULIFLOWER-MOSAIC VIRUS BY THREE
SPECIES OF APHIDS

Aphid species and number of insects per lot	Number of lots	First day		Second day		Third day	
		Seedlings inoculated	Seedlings infected	Seedlings inoculated	Seedlings infected	Seedlings inoculated	Seedlings infected
Cabbage aphid, <i>Brevicoryne brassicae</i> :							
1 per lot.....	3	18	4	18	0	18	0
5 per lot.....	1	6	2	6	0	6	0
10 per lot.....	1	7	7	7	0	7	0
20 per lot.....	7	42	34	42	0	42	0
Turnip aphid, <i>Rhopalosiphum pseudobrassicae</i> :							
20 per lot.....	6	40	16	40	0	40	0
Green peach aphid, <i>Myzus persicae</i> :							
5 per lot.....	2	10	2	10	0	10	0
20 per lot.....	9	55	29	55	0	55	0

for 30 days to successive healthy cauliflower seedlings. These preliminary tests are not tabulated, but no transmissions were obtained after the first day.

As shown in table 7, each of the three species of aphids transmitted the virus from diseased to healthy cauliflower during the first day; but none of the lots tested produced infection during the second or third day.

By Lots of 20 Aphids with Hourly Transfers. An attempt was made to determine more precisely how long the cabbage, turnip, and green peach aphids retained the cauliflower-mosaic virus. Each of 3 lots of 20 wingless, mature aphids of each species, reared on mosaic-infected cauliflower plants, was transferred hourly to 10 successive healthy plants.

As table 8 shows, 2 of 3 lots of 20 cabbage aphids transmitted the virus during the first and second hours and 1 lot during the first hour only. Each lot of the other two species of aphids transmitted the virus during the first hour only.

By Single Aphids in Short Feeding Time. Previously noninfective, mature, wingless aphids were starved for a period of 30 minutes in a stentor dish, with the bottom covered with moist filter paper. Each aphid was transferred with a moistened camel's-hair brush from the moist chamber to a mosaic-infected

cauliflower plant and allowed to feed for 5 or 10 minutes. Some of the aphids crawled about on the leaf, but after finding a suitable feeding place they settled down, with the antennae parallel to the body and the labium at right angles to the leaf and touching it. Each aphid was observed through a hand lens, and when it did not immediately withdraw the stylets, the feeding time was taken.

TABLE 8

RETENTION OF CAULIFLOWER-MOSAIC VIRUS BY THREE SPECIES OF
APHIDS TRANSFERRED HOURLY TO 10 SUCCESSIVE
HEALTHY CAULIFLOWER SEEDLINGS

Aphid species and lot no.	Number of aphids on first plant	Results on successive plants, with hourly transfers*										Last infection produced by aphids, hour
		1st	2d	3d	4th	5th	6th	7th	8th	9th	10th	
Cabbage aphid, <i>Brevicoryne brassicae</i> :												
Lot 1.....	20	+	+	-	-	-	-	-	-	-	-	2d
Lot 2.....	20	+	+	-	-	-	-	-	-	-	-	2d
Lot 3.....	20	+	-	-	-	-	-	-	-	-	-	1st
Turnip aphid, <i>Rhopalosiphum pseudobrassicae</i> :												
Lot 1.....	20	+	-	-	-	-	-	-	-	-	-	1st
Lot 2.....	20	+	-	-	-	-	-	-	-	-	-	1st
Lot 3.....	20	+	-	-	-	-	-	-	-	-	-	1st
Green peach aphid, <i>Myzus persicae</i> :												
Lot 1.....	20	+	-	-	-	-	-	-	-	-	-	1st
Lot 2.....	20	+	-	-	-	-	-	-	-	-	-	1st
Lot 3.....	20	+	-	-	-	-	-	-	-	-	-	1st
Total +.....	..	9	2	0	0	0	0	0	0	0	0
Total -.....	..	0	7	9	9	9	9	9	9	9	9

* The plus sign (+) indicates the production of the disease, and the minus (-) shows that no disease resulted.

The time occupied by each aphid in finding a suitable feeding place and settling down to feed, is referred to by Watson (1936) as the "penetration time," but probably should be designated as prepenetration time. The average prepenetration time was 5.1 minutes with the cabbage aphid, 3.6 minutes with the turnip aphid, and 4.7 minutes with the green peach aphid (table 9).

After feeding 5 or 10 minutes on a mosaic-infected cauliflower plant, each aphid was transferred to a healthy cauliflower seedling; and it was fed for 5 or 10 minutes. The aphid then was transferred to 5 more healthy cauliflower seedlings in succession and fed 10 minutes on each.

Three species of aphids were tested in this way. Table 9 shows the results with those aphids that transmitted the virus to at least one healthy cauliflower seedling. As this table shows, 25 cabbage aphids, 5 turnip aphids, and 5 green peach aphids, each tested singly, produced infections only in the first cauliflower seedling. One cabbage aphid after feeding 5 minutes on a diseased cauliflower seedling failed to infect the first two healthy cauliflower seedlings, but infected the third plant. One green peach aphid caused an infection of

TABLE 9
 RETENTION OF CAULIFLOWER-MOSAIC VIRUS BY SINGLE APHIDS
 TRANSFERRED AT 5- OR 10-MINUTE INTERVALS TO SIX
 SUCCESSIVE HEALTHY CAULIFLOWER SEEDLINGS

Aphid species and insect no.	Time on diseased cauliflower, minutes		Results* on successive plants, with 10 minutes† per plant					
	Prepenetra-tion time	Feeding time	1st plant†	2nd plant	3rd plant	4th plant	5th plant	6th plant
Cabbage aphid, <i>Brevicoryne brassicae</i> :								
No. 1.....	10	5	—	—	+	—	—	—
No. 2.....	13	10	+	—	—	—	—	—
No. 3.....	11	10	+	—	—	—	—	—
No. 4.....	11	10	+	—	—	—	—	—
No. 5.....	11	10	+	—	—	—	—	—
No. 6.....	7	10	+	—	—	—	—	—
No. 7.....	7	10	+	—	—	—	—	—
No. 8.....	7	10	+	—	—	—	—	—
No. 9.....	6	10	+	—	—	—	—	—
No. 10.....	6	10	+	—	—	—	—	—
No. 11.....	6	10	+	—	—	—	—	—
No. 12.....	5	10	+	—	—	—	—	—
No. 13.....	5	10	+	—	—	—	—	—
No. 14.....	5	10	+	—	—	—	—	—
No. 15.....	5	10	+	—	—	—	—	—
No. 16.....	5	10	+	—	—	—	—	—
No. 17.....	5	10	+	—	—	—	—	—
No. 18.....	4	10	+	—	—	—	—	—
No. 19.....	4	10	+	—	—	—	—	—
No. 20.....	4	10	+	—	—	—	—	—
No. 21.....	4	10	+	—	—	—	—	—
No. 22.....	4	10	+	—	—	—	—	—
No. 23.....	3	10	+	—	—	—	—	—
No. 24.....	2	10	+	—	—	—	—	—
No. 25.....	2	10	+	—	—	—	—	—
No. 26.....	1	10	+	—	—	—	—	—
Total or average.....	5.1	..	25+, 1-	26-	1+, 25-	26-	26-	26-
Turnip aphid, <i>Rhopalosiphum pseudobrassicae</i> :								
No. 1.....	7	10	+	—	—	—	—	—
No. 2.....	4	10	+	—	—	—	—	—
No. 3.....	3	10	+	—	—	—	—	—
No. 4.....	2	10	+	—	—	—	—	—
No. 5.....	2	10	+	—	—	—	—	—
Total or average.....	3.6	..	5+	5-	5-	5-	5-	5-
Green peach aphid, <i>Myzus persicae</i> :								
No. 1.....	7	5	+	—	+	—	—	—
No. 2.....	6	5	+	—	—	—	—	—
No. 3.....	6	5	+	—	—	—	—	—
No. 4.....	5	5	+	—	—	—	—	—
No. 5.....	3	5	+	—	—	—	—	—
No. 6.....	2	5	+	—	—	—	—	—
Total or average.....	4.7	..	6+	6-	1+, 5-	6-	6-	6-

* The plus sign (+) indicates the production of the disease, and the minus (-) shows that no disease resulted.

† The feeding time on the first plant was 5 minutes for cabbage aphid no. 1 and all green peach aphids; all other feeding periods on healthy plants were 10 minutes.

the first cauliflower plant, failed to infect the second, but infected the third. Negative results are not shown in table 9: 72 cabbage, 41 turnip, and 40 green peach aphids tested singly in short feeding periods failed to transmit the virus.

TABLE 10

LOSS AND RECOVERY OF INFECTIVITY BY APHIDS ON CAULIFLOWER PLANTS INOCULATED WITH CAULIFLOWER-MOSAIC VIRUS

Aphid species and first inoculated plant no.	Results* when a lot of 20 aphids was transferred from the first inoculated plant to a second healthy plant on the following day												Days to first symptom on first inoculated plant
	4th	5th	6th	7th	8th	9th	10th	11th	12th	13th	14th		
Cabbage aphid, <i>Brevicoryne brassicae</i> :													
Plant 1.....	-	-	+	+	+	+	+	+	+	+	+	-	18
Plant 2.....	-	-	-	-	-	+	-	+	+	-	-	-	20
Plant 3.....	-	-	-	-	-	-	-	+	-	-	-	-	21
Plant 4.....	-	-	-	-	-	+	+	+	-	-	-	-	24
Plant 5.....	-	-	-	-	-	-	+	+	+	+	+	-	25
Plant 6.....	-	-	-	-	-	-	+	-	-	-	-	-	30
Total +.....	0	0	1	1	1	3	4	5	3	2	3		
Total -.....	6	6	5	5	5	3	2	1	3	4	3		
Green peach aphid, <i>Myzus persicae</i> :													
Plant 7.....	-	-	-	+	-	+	-	-	-	-	-	+	30
Plant 8.....	-	-	-	-	-	+	-	-	-	-	-	+	33
Total +.....	0	0	0	1	0	0	0	0	0	0	0	2	
Total -.....	2	2	2	1	2	2	2	2	2	2	2	0	

The plus sign (+) indicates the production of the disease, and the minus (-) shows that no disease resulted.

RECOVERY OF VIRUS BY APHIDS FROM AN INOCULATED PLANT BEFORE SYMPTOMS DEVELOP

An attempt was made to determine whether the cabbage and green peach aphids were able to recover the virus from inoculated cauliflower plants before the first symptom of the disease developed. A large population of aphids reared on mosaic-infected cauliflower plants was transferred to a healthy cauliflower plant for 3 days. Each day from the fourth to the fourteenth day, one lot of 20 of these aphids was transferred from the plant so inoculated to a healthy cauliflower plant. Each lot of aphids remained on the second inoculated plant for 3 days and then the plant was fumigated to kill the aphids. The results reported in table 7 indicate that the aphids do not retain the virus longer than 1 day. Therefore the aphids were presumed to have lost their infectivity before transfer to the second healthy plant; and any transmission that occurred may be attributed to recovery of the virus from the first inoculated plant.

The transmissions by the two aphid species and also the incubation period of the disease, or the period for the earliest symptom (cleared veinlets) to develop in the original infected cauliflower plant, are shown in table 10. With the cabbage aphid, the elapsed time to the first recovery of the virus varied from 6 to 11 days. The incubation period of the disease in the original infected

cauliflower plants varied from 18 to 30 days. With the green peach aphid, the elapsed time to the first recovery of the virus was 7 days with one lot, 14 days with the other. The incubation periods of the disease in the original infected cauliflower plants were 30 and 33 days, respectively. Fourteen additional lots of aphids, not tabulated in table 10, failed to recover the virus from the fourth to fourteenth day.

The fact that no transmissions occurred on the fourth or fifth day supports the assumption that the aphids had lost the infectivity acquired on the original mosaic-infected plant before they were transferred to the second healthy plant. The results show that the aphids were able to recover the virus from the first inoculated plant before symptoms developed on it.

MECHANICAL INOCULATION WITH VIRUS EXTRACT FROM CRUSHED APHIDS

An attempt was made to transmit the cauliflower-mosaic virus with the centrifuged virus extract of crushed, infective cabbage aphids by mechanical inoculation of healthy cauliflower and annual stock plants. The centrifuged virus extract prepared from 10 grams of infective cabbage aphids crushed in 90 cc of sterile distilled water was inoculated in 10 healthy cauliflower seedlings and 10 annual stock plants. Four cauliflower and 8 annual stock plants were infected. In three other tests, 4.3, 4.0 and 0.68 grams of infective cabbage aphids were crushed in sterile distilled water. The results obtained with the virus extract inoculated into healthy cauliflower seedlings and annual stock plants were as follows: 4.3 grams, 20 plants inoculated remained healthy; 4.0 grams, 1 of 10 annual stock plants became infected, 10 cauliflower plants inoculated remained healthy; and 0.68 grams, 1 of 10 cauliflower seedlings became infected, 10 annual stock plants remained healthy. Of a total of 80 plants inoculated, 14, or 18 per cent, became infected.

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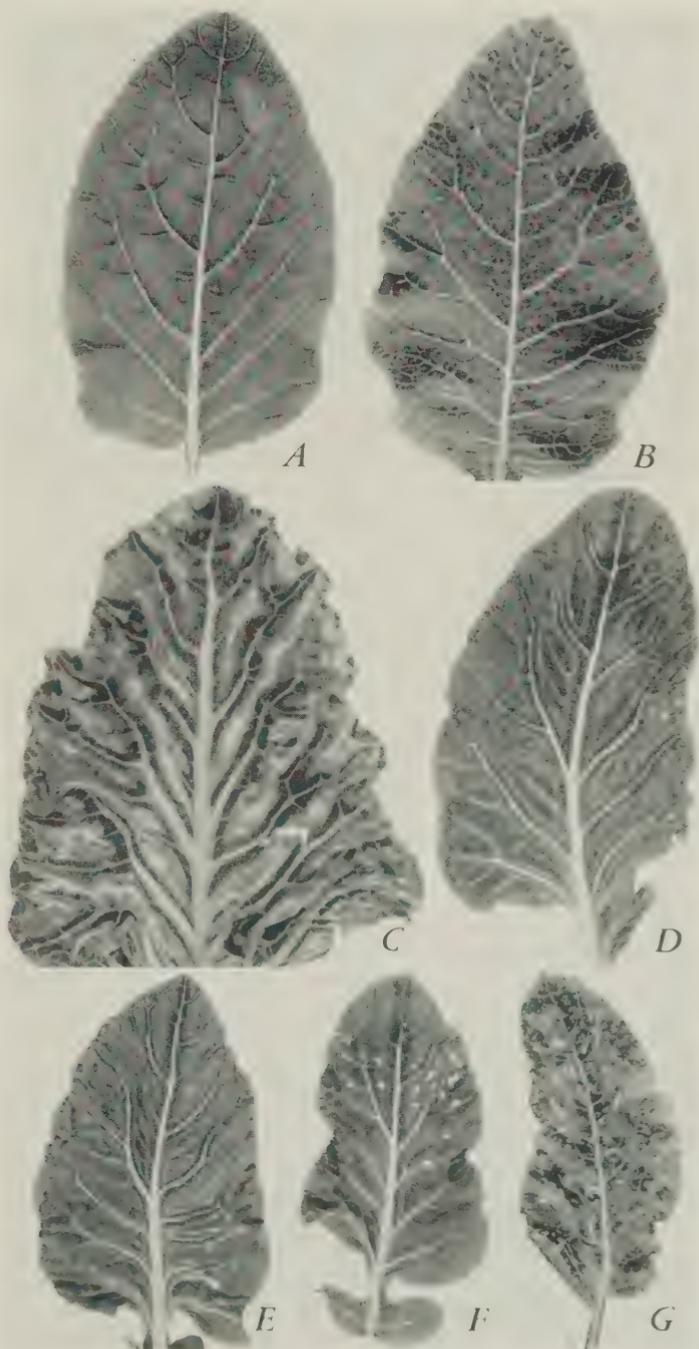


Plate 1. Symptoms of cauliflower mosaic on leaves of cauliflower (*Brassica oleracea* var. *botrytis*): A, leaf from healthy check or control plant; B, vein clearing; C, veinbanding, mottling, and distortion; D, curvature of the midrib; E, F, necrotic lesions; G, necrotic spotting, curvature of the midrib, and distortion.



Plate 2. SYMPTOMS OF MANGANESE TOXICITY ON STOCK PLANTS (*Manihot esculenta* var. *amarantha*). A, plant exhibited by excess of green-point apical (Mazata) disease, showing stunted growth and secondary slender roots from healthy root system removed from A; B, dying of rots; C, leaf showing faint, irregularly branching veins; D, leaf from plant infected with yellow-green (Physcomitrium) disease, showing similar symptoms to C; E, rottling; F, pale trichomes.

**THE MOST IMPORTANT SPECIES OF APHIDS
ATTACKING CRUCIFEROUS CROPS
IN CALIFORNIA**

E. O. ESSIG

THE MOST IMPORTANT SPECIES OF APHIDS ATTACKING CRUCIFEROUS CROPS IN CALIFORNIA¹

E. O. ESSIG²

APHIDS cause great damage to cruciferous crops—broccoli, brussels sprouts, cabbage, cauliflower, kale, mustard, radishes, turnips, and others. These insects weaken, stunt, and sometimes even kill the plants by sucking the juice. They may make cabbage, brussels sprouts, cauliflower, and broccoli wholly unfit to market, for it is difficult or impossible to remove them from the heads of such plants. On seed farms, they may completely destroy the plants before harvest by infesting the seedstalks. They cause even greater losses by transmitting plant viruses, which may destroy the plants over considerable areas.

Three aphid species that breed on these plants are responsible for most of the damage in California. These are the cabbage aphid, *Brevicoryne brassicae* (Linnaeus); the turnip or false cabbage aphid, *Rhopalosiphum pseudo-brassicae* (Davis); and the green peach aphid, *Myzus persicae* (Sulzer). All three species have become world wide in distribution and are to be found generally throughout the ranges of the host plants. This paper assembles the salient facts on their synonymy, characteristics, life histories, distribution, and host plants, as a basis for studies on their transmission of viruses and on their control.

THE CABBAGE APHID

Brevicoryne brassicae (Linnaeus) (Van der Goot, 1915, 1918)^{3, 4}

Aphis brassicae Linnaeus (1746, 1758)⁵

Aphis raphani Schrank (1801)⁶

Aphis insatidis Boyer de Fonscolombe (1841)⁷

Aphis floris-rapae Curtis (1860, p. 69-83)⁸

The cabbage aphid, *Brevicoryne brassicae* (Linnaeus) is usually more abundant on cruciferous crops than any other aphid and is therefore more injurious.

The cabbage aphid can be distinguished from other aphids by the large closely crowded colonies (fig. 1), the white waxy powdery covering over the bodies of the alate and apterous individuals, and the cruciferous host plant.

¹ Paper received for publication June 20, 1947.

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³ See "Literature Consulted" for citations, referred to in the text by author and date.

⁴ The genus *Brevicoryne* was proposed by B. Das and erected by Van der Goot in 1915 (1915 and 1918).

⁵ First referred to by Linnaeus in 1746 (1746) and described by him in 1758 (1758).

⁶ A synonym erected by Schrank (1801) for an aphid feeding on cabbage in Bavaria, Germany.

⁷ A synonym collected in the Province of Aix, France, previous to 1841, was described by Boyer de Fonscolombe (1841).

⁸ This species was described by Curtis in 1860 (1860, p. 69-83) and called the turnip flower plant louse. In this article Curtis lists the suggested control measures (tobacco decoctions, lime dust, hand-picking infested parts of plants) and discusses at length the insect predators and parasites of this aphid.

The turnip aphid has often been confused with this species; differences are discussed on pages 412-13.

Mounted specimens are readily distinguished by the long antennal segment III, which in the alates is covered with circular secondary sensoria; by the very short cornicles; the long slender tarsi; and the unguis, spur, or filament of the terminal antennal segment, which is four to five times as long as the base. Figures 2 and 3 show details of the male and three forms of females.

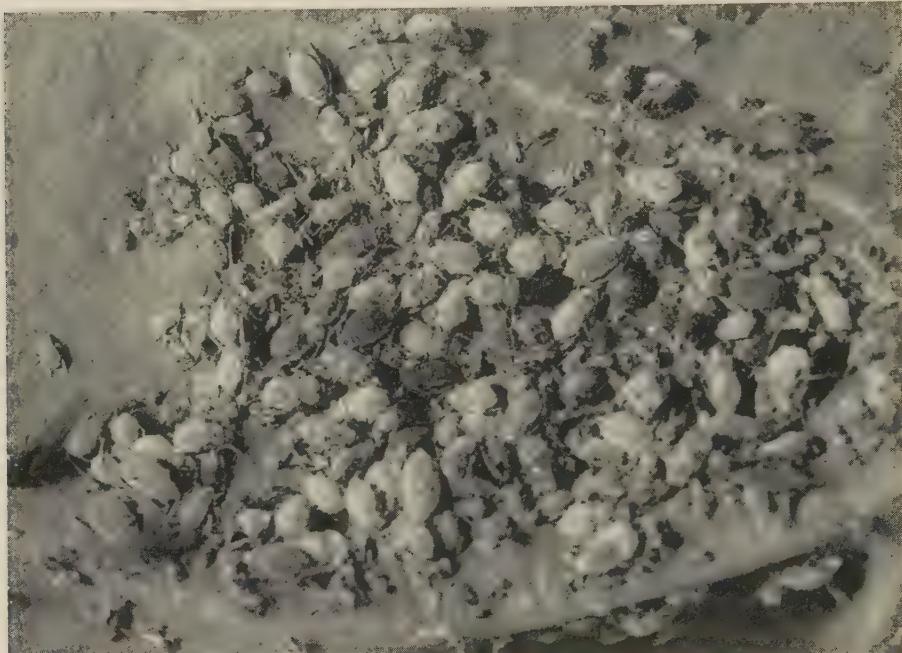


Fig. 1.—The cabbage aphid, *Brevicoryne brassicae* (Linn.): a typical colony on the underside of a cabbage leaf. The white powdery waxy covering is plainly shown on many individuals. ($\times 4$.)

Life History. In the warmer climates of the distribution of the cabbage aphid, there is continuous reproduction by parthenogenesis, and only apterous and alate parthenogenetic females occur. There may be as many as 30 or more generations during the year, so that extremely dense and destructive populations are built up. During the winter these populations may be slowed up and even reduced by cooler temperatures, rain, and other climatic factors. In California this aphid is found in prosperous colonies on wild mustard (*Brassica campestris*) and other native or weedy cruciferous plants. In summer and fall, many of the natural host plants disappear and the aphid is forced to cultivated crops, which may suffer severely from its attacks. Wherever summer rains occur, the native hosts continue to serve as reservoirs for feeding and breeding.

During spring—April and May—and fall—October and November—great numbers of winged migrants may be seen in California. They literally fill the air in certain areas along the foothills.

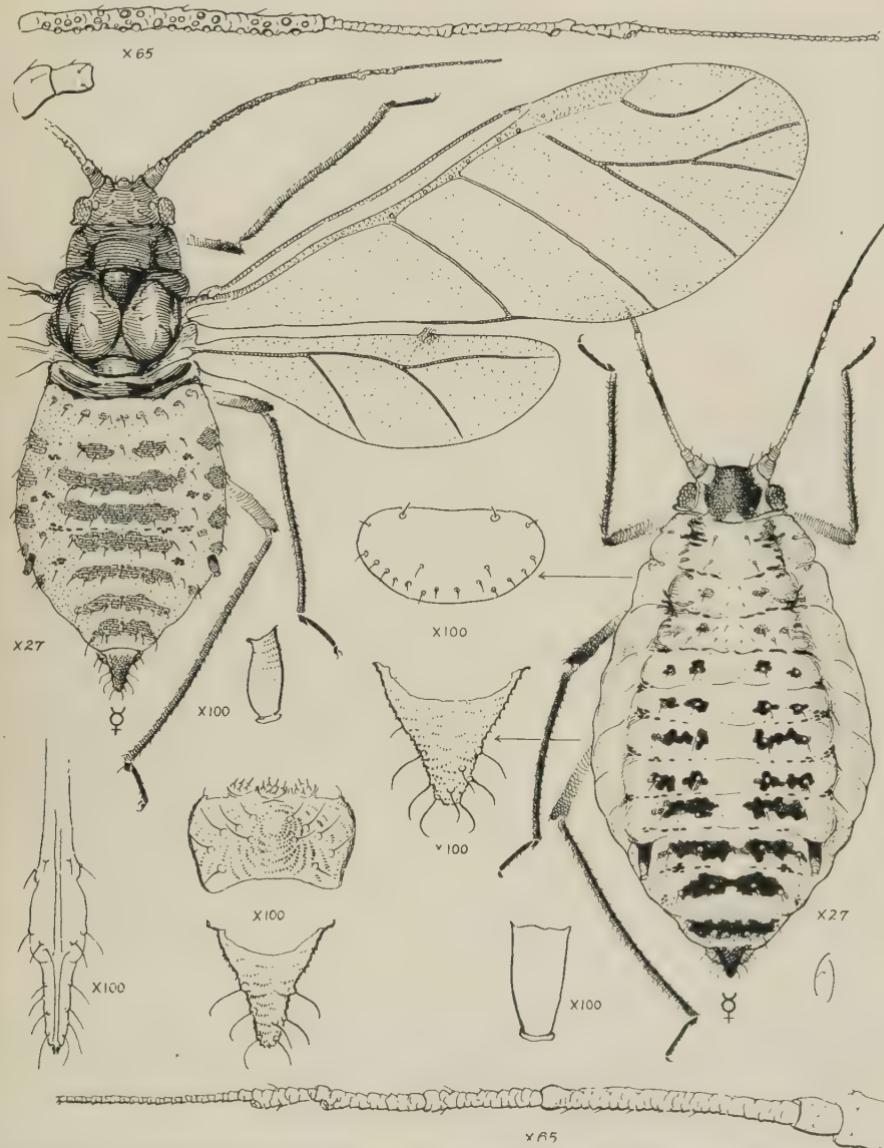


Fig. 2.—The cabbage aphid, *Brevicoryne brassicae* (Linn.): the alate and apterous viviparous females. The important body structures, including antennae, cornicles, anal plate, cauda, and tip of rostrum, used in identification, are greatly enlarged as indicated on the illustration. Note the long antennal segment III covered with sensoria and the long slender tarsi, which separate this aphid from others feeding on cruciferous plants. (Drawing by Frieda Abernathy.)

In the more northern reaches of its distribution, the spring and summer reproductives (migrants and alienicolae) are replaced in fall by sexuparae, or gynoparae. The sexuparae are apterous and alate viviparous parthenogenetic females that give birth to sexuales. Males and females of the sexuales (fig. 3)

mate, and the females lay eggs that survive the winter. Eggs of this aphid are usually laid on old stems or leaves of the cruciferous crops left in the fields. In northern Europe the eggs laid in October, November, and December hatch the following March, April, and May. Even in that climate a few adult viviparous females occasionally survive the winters, but ordinarily all of these perish,

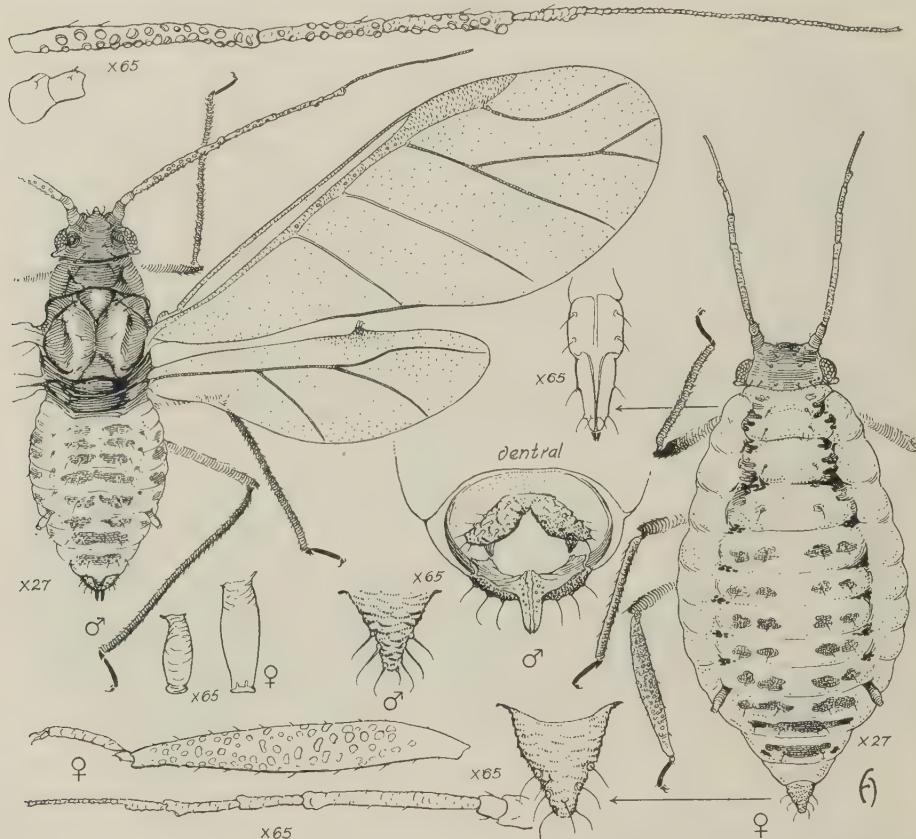


Fig. 3.—The cabbage aphid, *Brevicoryne brassicae* (Linn.): the alate male and the apterous oviparous female with important body structures used in identification greatly enlarged as indicated. The sensorialike structures on the swollen hind tibiae of the sexual female are characteristic of this sex. Note the numerous sensoria on antennal segments III, IV, and V of the alate male. (Drawing by Frieda Abernathy.)

and only the eggs remain to hatch in spring and give rise to the spring, summer, and fall colonies that are so destructive.

Host Plants. The host plants of the cabbage aphid belong almost entirely to the large, cosmopolitan family Cruciferae and include the following:

<i>Arabiopsis thaliana</i>	<i>Brassica caulorapa</i>	<i>Brassica juncea</i>
<i>Arabis glabra</i>	<i>Brassica chinensis</i>	<i>Brassica juncea</i> var. <i>crispifolia</i> (<i>B. japonica</i>)
<i>Barbarea vulgaris</i>	<i>Brassica erucastrum</i> (<i>Erucastrum pollichii</i>)	<i>Brassica kaber</i> (<i>B. campestris</i>)
<i>Brassica adpressa</i>	<i>Brassica fruticulosa</i>	<i>Brassica muralis</i>
<i>Brassica arvensis</i> (<i>Sinapis arvensis</i>)	<i>Brassica hirta</i> (<i>B. alba</i>)	

<i>Brassica napobrassica</i>	<i>Cardamine hirsuta</i>	<i>Mathiola incana</i>
<i>Brassica napus</i>	<i>Cochlearia anglica (C. arctica)</i>	<i>Mimulus guttatus</i>
<i>Brassica nigra</i>		<i>Myagrum perfoliatum</i>
<i>Brassica oleracea</i>	<i>Crambe sp.</i>	<i>Raphanus landra</i>
<i>Brassica oleracea</i> var. <i>acephala</i>	<i>Diplotaxis tenuifolia</i>	<i>Raphanus maritimus</i>
<i>Brassica oleracea</i> var. <i>geminifera</i>	<i>Eruca sativa</i>	<i>Raphanus raphanistrum</i>
<i>Brassica pekinensis</i>	<i>Erucastrum obtusangulum</i>	<i>Raphanus sativus</i> var. <i>longipinnatus</i>
<i>Brassica rapa</i>	<i>Erysimum canescens</i>	<i>Sinapis juncea</i> var. <i>nepiformis</i> (<i>Brassica napi</i> <i>formis</i>)
<i>Bunias erucago</i>	<i>Iberis sp.</i>	
<i>Cakile maritima (C. edentula)</i>	<i>Isatis tinctoria</i>	<i>Lepidium graminifolium</i>
<i>Capsella bursa-pastoris</i>	<i>Lepidium amplexicaule</i>	<i>Lepidium ruderale</i> [sic]
<i>Capsicum frutescens (C. annuum)</i>	<i>Lunaria annua</i>	<i>Lepidium sativum</i>
	<i>Mathiola bicornis</i>	<i>Sisymbrium officinale</i>
		<i>Sisymbrium sophia</i>

Some other plants reported as hosts are very questionable. They may have been only resting places for the dispersing or migrating alates.

Origin and Distribution. The cabbage aphid is one of the commonest species to be found throughout the temperate and subtropical regions of the world. This wide distribution has no doubt been made possible by the very extensive distribution and abundance of its cruciferous host plants. The many vegetables, ornamental flowering plants, and economic weeds have been carried through commerce to all inhabited lands and have become adapted in all except the most extreme climates.

The cabbage aphid has no doubt been associated with cultivated cruciferous crops in certain areas ever since they were developed by man. Its exact place of origin may never be definitely established. However, this insect appears to have first been associated with host plants originating in the Palaearctic Region and was early reported on wild and cultivated plants in Europe. It probably occurred on cabbages and related host plants long before it was recorded in print. Frisch (1734) is credited as having first brought this aphid to the attention of the public in 1734 when he reported it from Germany, described its work, and presented drawings that aid in its identification.

So far as I am able to ascertain, the cabbage aphid does not appear to be a serious pest of cruciferous crops in Asia. It is rarely found in lists of destructive insects from that continental area. Wu (1935) in his *Catalogus Insectorum Sinensium* does not list this species. Recently Ying-Tou Mao^w reviewed Chinese literature on aphids thoroughly, but found the cabbage aphid reported only from Hangchow, Fukien, and Taiwan. This species was not included in any of several large collections of aphids I have received from China. The shortage of records may simply indicate a lack of intensive study of this insect in China. Still, it is especially significant in view of the fact that many of the most important and useful members of the cabbage family originated in that country. It may be a further indication of the possible origin of the cabbage aphid in Northwestern Europe, the home of the cabbage.

The species does appear to be quite widely distributed in Japan and has been reported by many entomologists in that country.

From the information at hand, it appears possible that the cabbage aphid

^w Ying-Tao Mao. A list of Chinese aphids and their host plants. Typewritten manuscript.

may have originated in Western Europe in association with wild or sea cabbage, charlock, cabbage, cauliflower, brussels sprouts, kale, and other wild and cultivated cruciferous plants. Its counterpart in Asia and the Pacific islands appears to be the turnip aphid.

It is hardly practical to list all or even the larger geographical units throughout the world, especially in Africa and South America, where the cabbage aphid has been found. The following list has been compiled from many sources:

Asia: Astrakhan, Bessarabia, China (Amoy, Hangchow, Hopei, Kiangsu, Taiwan), Iraq, India (Lahore), Japan (Fukuoka, Hokkaido, Morioka), Palestine, Siberia, Syria, Transcaucasia

Africa: Bengal, Cape of Good Hope, Egypt, Eritrea, Kenya, Madagascar, Mauritius, Morocco, Nairobi, Natal, Nyassaland, Orange Free State, Rhodesia, Transvaal

Australia: Queensland, New South Wales, South Australia, Tasmania

New Zealand

Europe: Belgium, Czechoslovakia, France, Germany, Great Britain, Holland, Ireland, Italy, Lettland, Malta, Norway, Poland, Serbia, Spain, Sweden, U.S.S.R.

North America: Canada (British Columbia, Ontario, Quebec, and other provinces), United States (every state), West Indies (Cuba, Puerto Rico, Santo Domingo), Bermuda, Guatemala, Mexico

South America: Argentina, Brazil, Chile, Colombia, Virgin Islands

South Pacific: Fiji, Hawaii

THE TURNIP APHID¹⁰

Rhopalosiphum pseudobrassicae (Davis)

Aphis pseudobrassicae Davis (1914, p. 231)

Lipaphis pseudobrassicae (Davis) (Mordvilko, 1928, p. 200)

Aphis mathiolellae Theobald (1918) (Hall, 1926, p. 24)

The turnip or false cabbage aphid is almost as destructive to cruciferous crops as is the cabbage aphid. It appears to have originated in Asia, where it has a wide distribution. It has apparently been introduced into many other countries and has become widely distributed in many localities.

It was no doubt early confused with the cabbage aphid and became firmly established in most areas before it was recognized as a distinct species. In fact, its true identity was not discovered until 1914 when it was described as *Aphis pseudobrassicae* by Davis (1914, p. 231) from specimens collected by W. J. Schoene on cabbage at Geneva, New York on July 15, 1912, and on mustard and kale taken at Evansville, Indiana, November 20 of the same year. In September and October, 1913, additional material was taken on radish and turnip at Lafayette, Indiana, and on turnip at College Station, Texas, by F. B. Padock (1915).

In size and general appearance it greatly resembles the cabbage aphid. However, in California, it seems to have less powdery wax on its body. Specimens of whole colonies over large areas may appear bright green and almost devoid of the white waxy secretion so characteristic of the cabbage aphid. However, pulverulent forms do occur here. Specimens are paler in color than the cabbage aphid and lack the broad transverse broken dark bands on the dorsum of the alates and apterous forms; antennal segment III is much

¹⁰ This common name has also been used for the cabbage aphid, *Brevicoryne brassicae* (Linn.). The turnip aphid is also known as the false cabbage aphid.

shorter; tarsi are shorter; cornicles are longer; there are secondary sensoria present on antennal segment III and IV of the alates; the unguis, spur, or filament of the terminal antennal segment is three times the length of the base; and the cauda is triangular in shape. Important characters for identification are shown in figure 4.

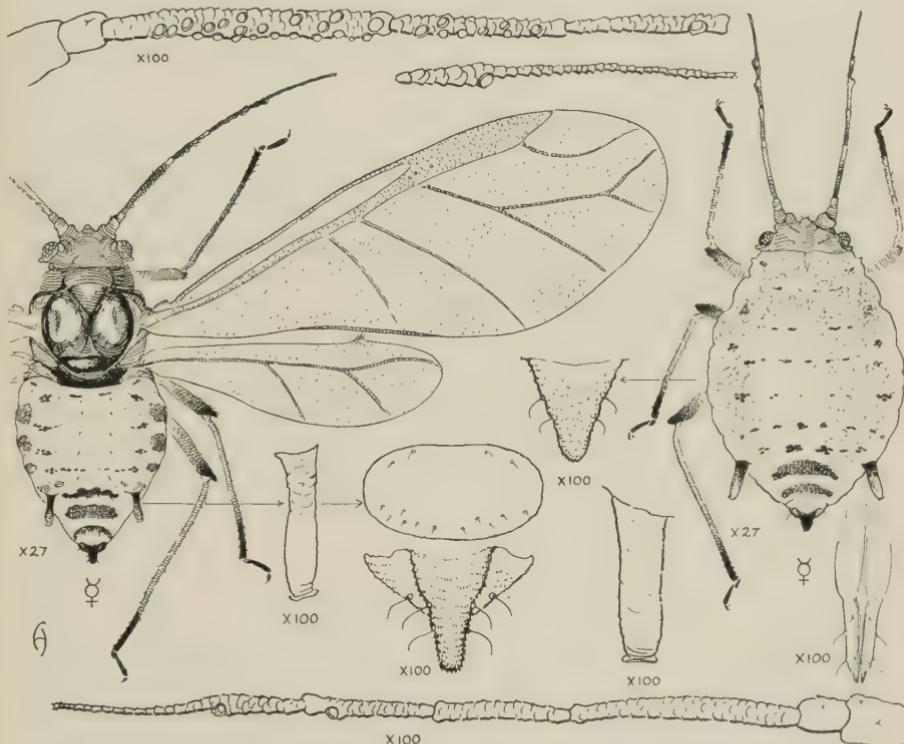


Fig. 4.—The turnip or false cabbage aphid, *Rhopalosiphum pseudobrassicae* (Davis): alate and apterous viviparous females with the antennae, cornicles, anal plates, caudas, and tip of rostrum greatly enlarged as indicated. Note the sensoria on both antennal segments III and IV of the alate. (Drawings by Frieda Albernathy.)

Life History. The life history is similar to that of the cabbage aphid. Allen and Harrison (1941) have studied the life history in the south and state that there are 15 to 46 generations a year; 50 to 100 young are produced by a single female; aphids live as long as 2 months; no sexuales appear in the south; living forms occur throughout the year; most damage is done during the winter months—October to and including the following March. The life history in the northern limits of distribution has not been studied and, although sexual forms are probably produced, they have not been reported.

Host Plants. The host plants are similar to those of the cabbage aphid, but are as yet not so well known. The following are reported to date:

Barbarea vulgaris
Brassica caulorapa
Brassica cernua

Brassica juncea (*B.*
rugosa)
Brassica kabera (*B.*
campestris)

Brassica napobrassica
Brassica napus
Brassica nigra

<i>Brassica oleracea</i>	<i>Chrysanthemum</i>	<i>Nasturtium officinale</i>
<i>Brassica oleracea</i> var. <i>acephala</i>	<i>coronarium</i> (?)	<i>(Roripa nasturtium)</i>
<i>Brassica oleracea</i> var. <i>botrytis</i>	<i>Descurainia sophia</i>	<i>Phaseolus</i> sp. (?)
<i>Brassica oleracea</i> var. <i>capitata</i>	<i>Gynandropsis speciosa</i> (?)	<i>Ranunculus sceleratus</i> (?)
<i>Brassica pekinensis</i>	<i>Lactuca sativa</i>	<i>Raphanus raphanistrum</i>
<i>Brassica rapa</i>	<i>Lepidium campestre</i>	<i>Raphanus sativus</i>
<i>Capsella bursa-pastoris</i>	<i>Lepidium virginicum</i>	<i>Raphanus sativus</i> var. <i>longipinnatus</i>
	<i>Lycopersicon esculen-</i>	<i>Thlaspi arvense</i>
	<i>tum</i> (?)	
	<i>Mathiola incana</i>	

Distribution. As previously indicated, this aphid probably originated in Asia and has spread by commerce throughout many other parts of the world. So far no records of its occurring in Europe have been noted in publications, which seems quite remarkable. The following distribution is known:

Asia: China (Chekiang, Hopei, Kiangsu, Kwangtung, Shantung, Taiwan), Korea (Sui-gan), India, Iraq, Japan (general, Daito Jina), Java, Loochoo, Siam, Sumatra

Africa: Egypt, Cape Colony, Maroc, Uganda

Australia: New South Wales

New Zealand

North America: Canada (British Columbia, Manitoba, Ontario, Quebec); United States (throughout much of the entire country: actually reported from Alabama, California—Berkeley, El Centro, Half Moon Bay, Lompoc, Los Angeles, Riverside, San Francisco, Stanford University, Stockton, Ventura—Connecticut, Florida, Georgia, Illinois, Indiana, Louisiana, Maine, Maryland, Mississippi, New Jersey, New York, North Carolina, Ohio, Pennsylvania, South Carolina, Tennessee, Texas, Virginia, Wisconsin), Bermuda, Puerto Rico

South America: Argentina, Trinidad

South Pacific: Hawaii (Hawaii, Oahu)

THE GREEN PEACH APHID¹¹

<i>Myzus persicae</i> (Sulzer)	<i>Aphis persicaecola</i> Boisduval (1867)
<i>Aphis persicae</i> Sulzer (1776, p. 105)	<i>Siphonophora achyrantes</i> Monell (1879)
<i>Aphis dianthi</i> Schrank (1801)	<i>Rhopalosiphum tulipae</i> Thomas (1879)
<i>Aphis vulgaris</i> Kyber (1815)	<i>Myzus malvae</i> Oestlund (1886)
<i>Aphis furcipes</i> Rafinesque (1817)	<i>Myzus pergandii</i> Sanderson (1901)
<i>Aphis rapae</i> Curtis (1842)	<i>Phorodon cyanoglossi</i> Williams (1910)
<i>Aphis vastator</i> Smee (1846)	<i>Rhopalosiphum solani</i> Theobald (1912)
<i>Aphis cyanoglossi</i> Walker (1848)	<i>Rhopalosiphum betae</i> Theobald (1913)
<i>Aphis egressa</i> Walker (1849)	<i>Rhopalosiphum lactucellum</i> Theobald (1915)
<i>Aphis redundans</i> Walker (1849)	<i>Rhopalosiphum tuberosellae</i> Theobald
<i>Aphis aucta</i> Walker (1849)	(1919)

The green peach aphid is without doubt the most important economic species in the entire family Aphididae. It is not only cosmopolitan in distribution and feeds on more varieties of host plants, but it is also capable of transmitting more kinds of plant viruses than any other insect known at the present time.

Description and Life History. Like most widely distributed aphids, the green peach aphid has a variable life history, not greatly different from that of the cabbage aphid. In the warmer tropical and subtropical areas, it is maintained by continuous generations of viviparous parthenogenetic fe-

¹¹ This aphid is called the tobacco aphid in Southern Rhodesia and other parts of Africa (Brain, 1940, p. 254).

males—both winged and wingless. There may be 30 to 40 generations a year, although the complete life history has not been accurately recorded in all areas. In the northern limits of its range, it is maintained chiefly by migrations from more favorable and warmer areas where it has persisted and multiplied even during the winter. The migrations or dispersals northward begin early in February, March, April, and May, and may continue until winter approaches. The advance northward is regulated by the increasingly favorable seasonal weather conditions. Escapes from greenhouses and even residences may also account for small isolated colonies which may appear in northern regions in advance of the regular migrations.

In quite cold northern climates the green peach aphid may give rise to sexuales, and eggs are produced that survive the winters and give rise to spring generations. The alternate winter hosts are usually fruit trees, including apricots, cherries, nectarines, peaches, and plums.

In California sexual forms are rarely taken. But males and females were collected on sand cherry, *Prunus pumila*, at Riverside by R. C. Dickson on December 20, 1940. They are probably quite common but are not readily discovered.

The various forms are:

Stem mother, a pink form that hatches from the overwintering egg and gives rise to succeeding generations.

Apterous viviparous female (fig. 5, B), a pale yellow or green form born from the stem mother and living on the primary host. She gives birth to winged spring migrants.

Spring migrants, greenish, yellowish, or reddish, black-marked winged viviparous females (fig. 5, A) that migrate from the winter primary hosts and settle on spring and summer hosts of all kinds. These may also migrate great distances, especially if carried by favorable winds. The apterous females are usually greenish and have the apical portions of the antennae and legs, and tips of cornicles dusky or black. The alates are yellowish or greenish, with the head, thorax, most of the antennae, apical portions of leg segments, bases of the cornicles, lateral spots, and a large median dorsal spot on the abdomen black. The swollen cornicles and black dorsal abdominal spot serve to identify this aphid readily.

Summer alate and apterous viviparous females are not unlike the spring migrants. They are produced through many generations on the summer hosts and disperse freely over wide areas. According to Proftt (1939, p. 14–15) winged adults have been found on islands 36 miles from the North Sea coast of Germany and on Spitzbergen, hundreds of miles from their normal habitat. The progeny of these may survive the winters in favorable areas.

Fall migrants, usually darker specimens that migrate to the primary host plants, where they mate and give rise to alate males and apterous sexual females. The latter lay the overwintering eggs.

Males, small, very dark, almost wholly black.

Oviparous females, apterous, not greatly different from the apterous viviparous females.

Host Plants. It will probably never be possible to secure an all-inclusive list of the host plants of this aphid. Its feeding habits are so varied that its

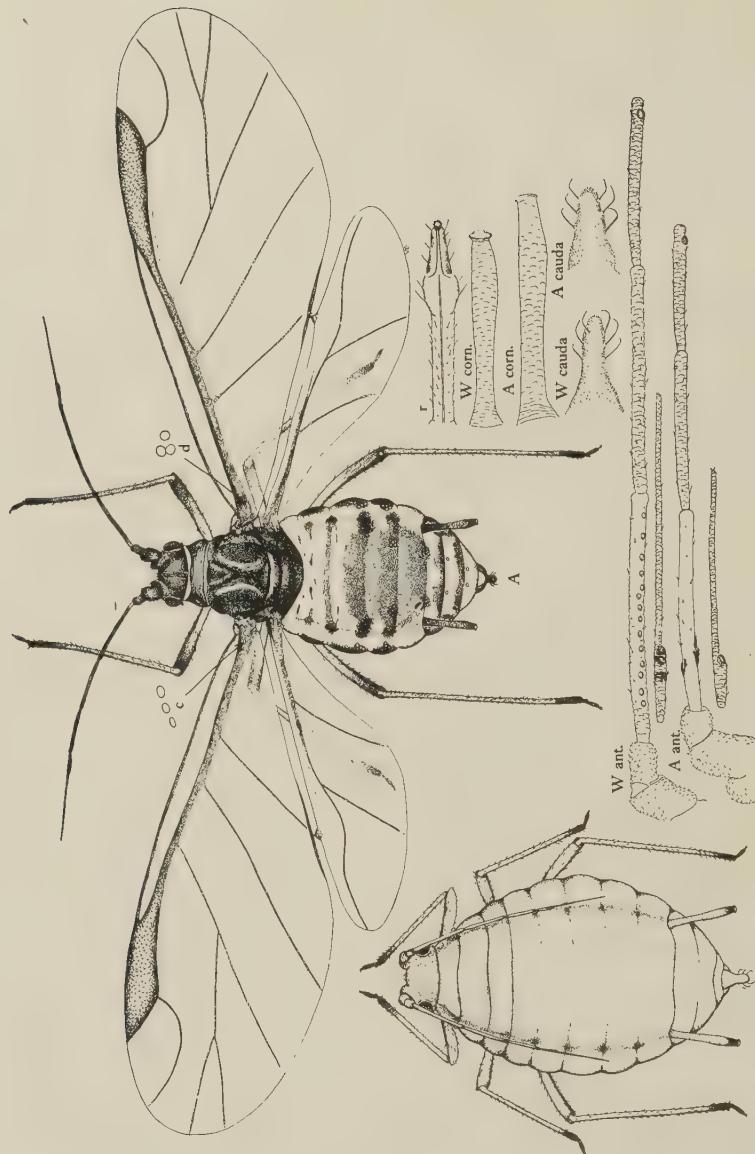


Fig. 5.—The green peach aphid, *Myzus persicae* (Sulzer): A, Adult alate viviparous female: c and d, fenestras or small transparent pores at the bases of the forewings; r, rostrum; W corn., antenna; W ant., antennae; W cauda, cauda. B, Adult apterous viviparous female: A ant., antennae; A cauda, cauda. All greatly enlarged.

capacity for acquiring new hosts seems to be unlimited. The following list is as complete as facilities at hand permit:

<i>Abutilon</i> sp.	<i>Capsicum dulce</i>	<i>Cyclamen europaeum</i>
<i>Acalypha boemeroides</i>	<i>Capsicum frutescens</i>	<i>Cyclamen indicum</i>
<i>Acanthus spinosus</i>	(<i>C. annuum</i>)	<i>Cynara cardunculus</i>
<i>Acer negundo</i>	<i>Carduus</i> sp.	<i>Cynoglossum grande</i>
<i>Acer nuttali</i> [sic]	<i>Carica papaya</i>	<i>Cyrtanthus</i> sp.
<i>Achyranthes</i> sp.	<i>Carthamus tinctorius</i>	<i>Cytisus</i> sp.
<i>Aeraria cannabina</i> (<i>A.</i> <i>cuspidata</i>)	<i>Catalpa speciosa</i>	<i>Dalbergia sissoo</i> .
<i>Ageratum conyzoides</i>	<i>Centaurea</i> sp.	<i>Daphne</i> sp.
<i>Alternanthera</i> sp.	<i>Centranthus ruber</i>	<i>Datura stramonium</i>
<i>Althaea rosea</i>	<i>Cerastium semidecan-</i> drum	(<i>D. tatula</i>)
<i>Amaranthus</i> spp.	<i>Cestrum fasciculatum</i> var. <i>newellii</i>	<i>Daucus carota</i>
<i>Ammannia</i> sp.	<i>Cestrum pseudoquina</i>	<i>Dianthus caryophyllus</i>
<i>Amsinckia spectabilis</i>	<i>Chaerophyllum aro-</i> maticum	<i>Dianthus chinensis</i>
<i>Anthemis cotula</i>	<i>Chaerophyllum hirsutum</i>	<i>Digitalis lutea</i>
<i>Antirrhinum majus</i>	<i>Chaerophyllum roseum</i>	<i>Digitalis purpurea</i>
<i>Apium graveolens</i>	<i>Cheiranthus cheiri</i>	<i>Dipsacus fullonum</i>
<i>Aquilegia canadensis</i>	<i>Chenopodium album</i>	<i>Dyssodia</i> sp.
<i>Aquilegia vulgaris</i>	<i>Chenopodium murale</i>	<i>Duranta repens</i> (<i>D. plumieri</i>)
<i>Arctium lappa</i>	<i>Chenopodium viride</i> [sic]	<i>Echinops echinatus</i>
<i>Arctium majus</i>	<i>Chrysanthemum balsamita</i>	<i>Emilia sonchifolia</i>
<i>Asclepias speciosa</i>	<i>Chrysanthemum coccineum</i>	(<i>Senecio sonchifolius</i>)
<i>Asparagus officinalis</i>	<i>Chrysanthemum frutescens</i>	<i>Erigeron canadensis</i>
<i>Asparagus plumosus</i>	<i>Chrysanthemum indicum</i>	<i>Erodium botrys</i>
<i>Asparagus sprengeri</i>	<i>Cichorium endivia</i>	<i>Erodium cicutarium</i>
<i>Astragalus</i> sp.	<i>Citrullus vulgaris</i>	<i>Eruca sativa</i>
<i>Atriplex</i> sp.	<i>Citrus aurantium</i>	<i>Erythronium dens-canis</i>
<i>Atropa belladonna</i>	<i>Citrus limonia</i>	<i>Escallonia pulvlerulenta</i>
<i>Aubrieta</i> sp.	<i>Citrus maxima</i>	<i>Euonymus communis</i>
<i>Barbarea vulgaris</i>	<i>Citrus medica</i>	<i>Euphorbia helioscopia</i>
<i>Bauhinia variegata</i>	<i>Clarkia elegans</i>	<i>Ficus pumila</i>
<i>Bellis perennis</i>	<i>Clarkia pulchella</i>	<i>Foeniculum vulgare</i>
<i>Bellis silvestris</i>	<i>Cnicus</i> sp.	<i>Fragaria chiloensis</i>
<i>Beloperone</i> sp.	<i>Cochlearia armoracia</i> (<i>Nas-</i> <i>turtium armoracia</i>)	<i>Freesia</i> sp.
<i>Beta vulgaris</i> (<i>B.</i> <i>bengalensis</i>)	<i>Codiaeum</i> sp. (<i>Croton</i> sp.)	<i>Fuchsia coccinea</i>
<i>Bougainvillea campestris</i>	<i>Colocasia</i> sp.	<i>Fuchsia macrantha</i>
<i>Bougainvillea juncea</i>	<i>Convolvulus arvensis</i>	<i>Fuchsia magellanica</i> var. <i>globosa</i>
<i>Bougainvillea spectabilis</i>	<i>Convolvulus crispus</i>	<i>Galactites tomentosa</i>
<i>Brassica kaber</i> (<i>B.</i> <i>arvensis</i>)	(<i>Ipomoea crispa</i>)	<i>Galium mollugo</i>
<i>Brassica napus</i>	<i>Coprosma baueri</i>	<i>Geranium molle</i>
<i>Brassica nigra</i>	<i>Cordyline</i> sp.	<i>Geranium robertianum</i>
<i>Brassica oleracea</i>	<i>Coronopus didymus</i>	<i>Gladiolus</i> sp.
<i>Brassica pekinensis</i>	<i>Crataegus</i> sp.	<i>Gloxinia digitaliflora</i>
<i>Brassica rapa</i>	<i>Crepis tectorum</i>	<i>Glycine</i> sp.
<i>Buddleia madagascari-</i> <i>ensis</i>	<i>Crocus</i> sp.	<i>Gnaphalium spathulatum</i>
<i>Buddleia orientalis</i> [sic]	<i>Crotalaria laburnifolia</i>	<i>Godetia amoena</i>
<i>Calceolaria</i> sp.	<i>Crotalaria mucronata</i>	<i>Gossypium herbaceum</i>
<i>Calendula arvensis</i>	<i>Cryptostemma calendulaceum</i>	<i>Grindelia robusta</i>
<i>Calendula officinalis</i>	<i>Cucumis melo</i>	<i>Hedera helix</i>
<i>Camellia japonica</i>	<i>Cucurbita maxima</i>	<i>Helianthus annuus</i>
<i>Canna indica</i>	<i>Cucurbita moschata</i>	<i>Helichrysum bracteatum</i>
<i>Capsella bursa-pastoris</i>	<i>Cucurbita pepo</i>	<i>Heliotropium arborescens</i> (<i>H. peruviana</i>)
		<i>Hemerocallis</i> sp.

<i>Hibiscus abelmoschus</i> (<i>H.</i> <i>moschatus</i> ; <i>Abelmoschus</i> <i>moschatus</i>)	<i>Moraea iridioides</i>	<i>Prunus besseyi</i>
<i>Hibiscus esculentus</i>	<i>Myosotis scorpioides</i>	<i>Prunus cerasus</i>
<i>Hibiscus roseus</i>	<i>Myrtus</i> sp.	<i>Prunus domestica</i>
<i>Hordeum</i> sp.	<i>Narcissus</i> sp.	<i>Prunus domestica</i> var. <i>insititia</i>
<i>Humulus lupulus</i>	<i>Nasturtium armoracea</i>	<i>Prunus mume</i>
<i>Hyacinthus orientalis</i>	<i>Nasturtium indicum</i>	<i>Prunus persica</i>
<i>Hydrangea</i> sp.	<i>Nasturtium officinale</i> (<i>Radí-</i> <i>cula nasturtium-aquaticum</i> , <i>Roripa nasturtium</i>)	<i>Prunus serotina</i>
<i>Ilex</i> sp.	<i>Nemesia strumosa</i>	<i>Prunus virginiana</i>
<i>Ionidium concolor</i>	<i>Nemophila heterophylla</i>	<i>Prunus virginiana</i> var. <i>melanocarpa</i>
<i>Ipomoea batatas</i>	<i>Nerium indicum</i> (<i>N. odoratum</i>)	<i>Psidium guajava</i>
<i>Ipomoea maxima</i> [sic]	<i>Nerium oleander</i>	<i>Pulicaria dysenterica</i>
<i>Ipomoea purpurea</i> (<i>Con-</i> <i>volvulus major</i>)	<i>Nicotiana rustica</i>	<i>(Inula dysenterica)</i>
<i>Iresine lindenii</i>	<i>Nicotiana tabacum</i>	<i>Quamoclit lobata</i>
<i>Iris</i> sp.	<i>Onopordum acanthium</i>	<i>Radicula curvisiliqua</i>
<i>Justicia alba</i> [sic]	<i>Opuntia</i> sp.	<i>Ranunculus asiaticus</i>
<i>Kalanchoë</i> sp. (<i>Bryophyllum</i> sp.)	<i>Orobanche</i> sp.	<i>Ranunculus bulbosus</i>
<i>Kleinia nerifolia</i>	<i>Orthocarpus erianthus</i>	<i>Raphanus raphanistrum</i>
<i>Lactuca oldhamii</i>	<i>Oxalis cernua</i>	<i>Raphanus sativus</i>
<i>Lactuca sativa</i>	<i>Oxalis corniculata</i>	<i>Rapistrum rugosum</i>
<i>Lactuca scariola</i>	<i>Oxalis rosea</i>	<i>Rheum rhabonticum</i>
<i>Lactuca spicata</i>	<i>Panax lancasteri</i> [sic]	<i>Ribes odoratum</i>
<i>Lamium</i> sp.	<i>Papaver somniferum</i>	<i>Richardia africana</i>
<i>Lantana</i> sp.	<i>Parthenium argentatum</i>	<i>Ricinus communis</i>
<i>Lathyrus odoratus</i> (<i>Pisum odorata</i>)	<i>Pastinaca sativa</i>	<i>Rosa</i> sp.
<i>Lavatera assurgentiflora</i>	<i>Paulownia</i> sp.	<i>Rudbeckia laciniata</i>
<i>Lepidium draba</i>	<i>Penstemon spectabilis</i>	<i>Rumex dentatus</i>
<i>Ligustrum vulgare</i>	<i>Requeria trinervia</i> [sic]	<i>Sagina subulata</i>
<i>Lilium candidum</i>	<i>Petasites tricholobus</i>	<i>Salix</i> sp.
<i>Lilium longiflorum</i>	<i>Petunia hybrida</i>	<i>Salsola kali</i> (<i>S. tragus</i>)
<i>Linaria</i> sp.	<i>Pharbitis nil</i>	<i>Salvia leucantha</i>
<i>Liriodendron tulipifera</i>	<i>Phaseolus vulgaris</i>	<i>Salvia mellifera</i>
<i>Lupinus termis</i>	<i>Philadelphus coronarius</i>	<i>Sambucus canadensis</i>
<i>Lycopersicon esculentum</i> (<i>Solanum lycopersicum</i>)	<i>Physalis virginiana</i>	<i>Sanguisorba officinalis</i>
<i>Malus communis</i> (<i>Pyrus malus</i>)	<i>Picris echioides</i>	<i>Sanicula menziesii</i>
<i>Malva parviflora</i>	<i>Pimelea</i> sp.	<i>Saxifraga splendens</i> [sic]
<i>Malva rotundifolia</i>	<i>Pimenta officinalis</i>	<i>Secale cereale</i>
<i>Malvastrum coccineum</i>	<i>Pisum sativum</i>	<i>Sedum artissimum</i>
<i>Markhamia platycalyx</i>	<i>Pisum sativum</i> var. <i>arvense</i>	<i>Senebiera pinnatifida</i>
<i>Marsilea quadrifolia</i>	<i>Pittosporum eugeniooides</i>	<i>Senecio alpestris</i> (<i>S. crass-</i> <i>ifolius</i>)
<i>Marsilea vestita</i>	<i>Pittosporum tobira</i>	<i>Senecio cruentus</i>
<i>Matricaria inodora</i>	<i>Pittosporum undulatum</i>	<i>Senecio elegans</i>
<i>Mathiola</i> sp.	<i>Plantago</i> sp.	<i>Senecio jacobaea</i>
<i>Maurandia hendersoni</i> [sic]	<i>Poa</i> sp.	<i>Senecio mikanioides</i>
<i>Mazus</i> sp.	<i>Polygonum hydropiper</i>	<i>Senecio renifolius</i>
<i>Melianthus major</i>	<i>Polygonum multiflorum</i>	<i>(Cineraria renifolia)</i>
<i>Melilotus indica</i>	<i>Polygonum persicaria</i>	<i>Senecio vulgaris</i>
<i>Mentha aquatica</i> (<i>M. hirsuta</i>)	<i>Portulaca oleracea</i>	<i>Sesamum orientale</i>
<i>Mercurialis annua</i>	<i>Primula forbesii</i>	<i>Setaria viridis</i>
<i>Mesembryanthemum</i> sp.	<i>Primula polyantha</i>	<i>Silene</i> sp.
<i>Mimulus</i> sp.	<i>Primula vulgaris</i>	<i>Sisymbrium canescens</i>
<i>Montia perfoliata</i>	<i>Prunella vulgaris</i>	<i>Sisymbrium irio</i>
	<i>Prunus americana</i>	<i>Solandra grandiflora</i>
	<i>Prunus amygdalus</i> (<i>P. communis</i>)	<i>Solanum carolinense</i>
	<i>Prunus armeniaca</i>	<i>Solanum dulcamara</i>
	<i>Prunus avium</i>	<i>Solanum melongena</i>

<i>Solanum nigrum</i>	<i>Tragopogon</i> sp.	<i>Valerianella olitoria</i>
<i>Solanum pseudo-capsicum</i>	<i>Tribulus terrestris</i>	(<i>Valeriana olitoria</i>)
<i>Solanum tuberosum</i>	<i>Trifolium pratense</i>	<i>Verbena chamaedryfolia</i>
<i>Sonchus asper</i>	<i>Trifolium repens</i>	<i>Viburnum opulus</i>
<i>Sonchus oleraceus</i>	<i>Triticum aestivum</i> (<i>T. sati-</i>	<i>Vicia</i> sp.
<i>Spinacia oleracea</i>	<i>vum, T. vulgare</i>)	<i>Vinca major</i>
<i>Stellaria aquatica</i>	<i>Tropaeolum majus</i>	<i>Vinca minor</i>
<i>Stellaria media</i>	<i>Tulipa</i> spp.	<i>Viola odorata</i>
<i>Stizolobium deerlingianum</i>	<i>Typha</i> sp.	<i>Viola tricolor</i>
<i>Syringa vulgaris</i>	<i>Ulmus procera</i> (<i>U.</i>	<i>Vitis</i> sp.
<i>Tamarix</i> sp.	<i>campestris</i>)	<i>Withania somnifera</i>
<i>Taraxacum officinale</i>	<i>Umbellularia californica</i>	<i>Zea mays</i>
<i>Thalictrum minus</i>	<i>Ursinia</i> sp. (<i>Sphenogyne</i> sp.)	<i>Zelkova formosana</i> [sic]
<i>Tilia americana</i>	<i>Urtica pilulifera</i>	
<i>Townsendia exscapa</i>	<i>Urtica urens</i>	
(<i>T. sericea</i>)	<i>Valeriana pyrenaica</i>	

Distribution. The green peach aphid appears to be present throughout the entire world wherever agricultural crops are grown. It does not occur in the extreme cold areas of the Arctic Region nor in certain of the very hot desert oases. Whether this wide distribution is natural or aided by man cannot now be determined. Nevertheless man has indeed had a great influence in extending both its distribution and diet by the extensive development of agriculture in areas which were previously certainly not adapted to the requirements of this aphid.

In California it occurs in every county and is a pest on plants in houses, greenhouses, lathhouses, and out doors throughout the year in most localities.

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